Sexual size dimorphism in some montane forest passerines from south-central Africa

by R. J. Dowsett

Received 9 August 1982

The number of bird species in montane forests in Africa is notably less than that in lowland forest (Moreau 1966), and it has been suggested that montane species occupy broader niches. One way in which this might be accomplished is for there to be a significant difference in body size between the sexes of a species, enabling the species to exploit a greater range of food items. This paper examines mensural data from some African montane forest birds with this problem in mind.

Forty-three bird species breed regularly in the evergreen forests of the southwestern Nyika Plateau in northern Malawi and adjacent Zambia (Dowsett-Lemaire in press), 24 of them comprising the understorey avifauna of my main study area on the Nyika. All 24 species were caught in mist nets and ringed during population studies, particularly between 1979 and 1982, mostly at an altitude of 2100-2200 m.

Birds were weighed on each capture, and the wing-length of each individual measured at least once each year. Weights were taken to 0.1 g in the passerines considered in this paper, using Pesola balances whose accuracy was checked at intervals. Wing measurements (to 0.5 mm) were taken by the maximum chord method (Svensson 1975). Each bird was examined for moult, and those found to be moulting the longest primary feathers are excluded from the wing-length measurements analysed here.

Determination of sex

Sexual dimorphism in plumage exists in 11 of the 43 species in the Nyika forests, but only 4 of these are passerines resident in the understorey and thus able to be caught in any numbers: Cape Batis *Batis capensis,* Green-headed Sunbird *Nectarinia verticalis,* Eastern Double-collared Sunbird *N. mediocris* and Red-faced Crimson-wing *Cryptospiza reichenovii* (nomenclature follows Benson *et al.* (1971), amended by Dowsett & Dowsett-Lemaire (1980)). Of these 4 dichromatic species, the Cape Batis has a yearling plumage which for both sexes closely resembles the adult female dress. The remaining 20 species of the understorey are for all practical purposes monochromatic, although in the Starred Robin *Pogonocichla stellata* breeding males can be separated from females by the blue-grey of their heads being slightly glossed.

Because of these morphological similarities, therefore, I initially sexed birds of each species only by examination of the cloacal area of sexually active individuals (see Dowsett-Lemaire & Collette 1980). By this method, females could be recognized for at least one month during the breeding season and males for at least 3 months—in the Starred Robin, for example, males had greatly enlarged penile protuberances between mid-September and early January. All these species are strictly seasonal breeders on the Nyika (Dowsett & Dowsett-Lemaire in prep.), and as they were most easily mist-netted at that time, the great majority of individuals could be sexed with

certainty. Other characters (e.g. song, presence of a brood patch, etc.) were not used, as they need not be the prerogative of one sex alone.

Wing-lengths of the large number of birds sexed by cloacal examination were then analysed to see if there was a relationship between sex and wing-length. Thirteen species were sexed in numbers large enough for Student's t-test to be used (those species in Table 1 with a sample of at least 10 of each sex). Eleven of these showed highly significant differences ($P < 0.001$), with males notably longer-winged than females: only in the Cape Batis and Red-faced Crimson-wing were there no significant differences. Consequently, it was possible also to sex by wing-length most of those individuals of these 11 species which were caught when sexually inactive, although there remained some whose measurements fell within the area of overlap between the sexes.

TABLE 1

Sexual difference in wing-length (mm) in some montane forest birds in south-central Africa

	Adult male				Adult female				%[2]
	n	range	mean	±S.D.[1]	n	range	mean	±S.D.	overlap
Alcippe abyssinica	4	68–71	70.0	—	4	66–70	67.8	—	37
Andropadus tephrolaemus	38	97–102	99.0	0.97	91	87–95	92.3	2.05	0
Phyllastrephus flavostriatus	11	93–102	96.1	2.18	13	80.5–88	83.4	1.77	0
Alethe fuelleborni	17	106–112	107.9	1.70	11	103–107	104.6	1.12	23
Cossypha anomala	29	76–80.5	78.3	1.30	42	70–77.5	73.8	1.53	22
C. caffra	36	85–93	88.7	1.68	26	78–85	82.4	1.60	12
Pogonocichla stellata	128	79–87	82.6	1.67	108	72–80.5	76.3	1.52	4
Turdus olivaceus	11	117–128	122.4	3.68	14	110–120	114.6	2.79	4
Chloropeta similis	8	56.5–63	60.6	—	6	57–60	59.1	—	57
Apalis thoracica	19	55–61	57.2	1.65	26	50.5–56	53.7	1.31	32
Batis capensis	35	60–66	62.7	1.43	33	59.5–64	61.8	1.12	90
Elminia albonotata	17	66–70.5	68.1	1.13	19	61.5–66	64.2	1.10	6
Laniarius fuelleborni	6	87.5–91	88.9	—	5	81–84	82.9	—	0
Nectarinia verticalis	5	67–70.5	68.3	—	4	59–65.5	63.0	—	0
N. mediocris	48	55–65	58.7	1.56	41	52–55.5	53.8	0.77	20
Zosterops senegalensis	96	57.5–63	60.1	1.19	96	55.5–62	58.7	1.50	92
Cryptospiza reichenovii	23	54.5–59	56.3	1.02	22	54.5–57.5	56.1	0.82	96

1. Standard deviation not computed for samples of less than 10.
2. The right hand column shows the proportion of the total sample which falls in the area of overlap.

TABLE 2

Changes in wing-lengths of individual adult Starred Robins *Pogonocichla stellata* measured in subsequent years

		Mean sample wing-lengths (mm)			Statistical differences[2]	
	n[1]	Year	mean	Year	mean		
Male	43	1	82.55	2	82.79	n.s.	$P > 0.1$
	13	2	82.96	3	82.77	ditto	
	23	1	82.98	3	83.02	ditto	
Female	32	1	76.49	2	76.59	n.s.	$P > 0.1$
	9	2	76.83	3	76.94	ditto	
	19	1	76.32	3	76.50	ditto	

1. Number of individuals for which measurements are available in each of 2 years: year 1 (1979–80), 2 (1980–81), 3 (1981–82).
2. Student's t-test; n.s. = not significant.

Because of the confusing yearling plumage in the Cape Batis, only females sexed by cloacal examination are included in Table 1. This is the case also with the White-chested Alethe *Alethe fuelleborni*, in which yearlings resemble adults but retain the shorter remiges of the juvenile, so that the wing-lengths of some first-year males are likely to fall within the range of adult females. In the Starred Robin, wing-lengths increase by 3–4 mm or 4–5% on moult

into adult dress (n = 26), but in that species yearlings have a distinctive plumage quite unlike that of the monochromatic adults.

Even when adult, a bird's wing-length may vary from one annual moult to the next, but usually only to a small extent in passerines, and not sufficiently to influence any overall sexual differences. Table 2 shows that there were no significant changes in the mean wing-length of samples of individual Starred Robins measured at intervals of one and of 2 years. However, Thorne (1975) did show that in large samples of European Reed Warblers *Acrocephalus scirpaceus* there were small but significant increases in wing-length with age (of about 0.5 mm or 0.8% p.a.). Most other studies have shown no apparent increase with age (Flegg & Cox 1977, Stewart 1963).

Wear through abrasion during the year also has only a small effect: the wing-lengths of 3 adult male Starred Robins were reduced by 0.5–1.0 mm (0.6–1.2%) between the end of moult and the start of breeding, i.e. over a period of about 6 months. Most birds in the present study were measured during the breeding season, and so most data are strictly comparable as far as the degree of wear is concerned.

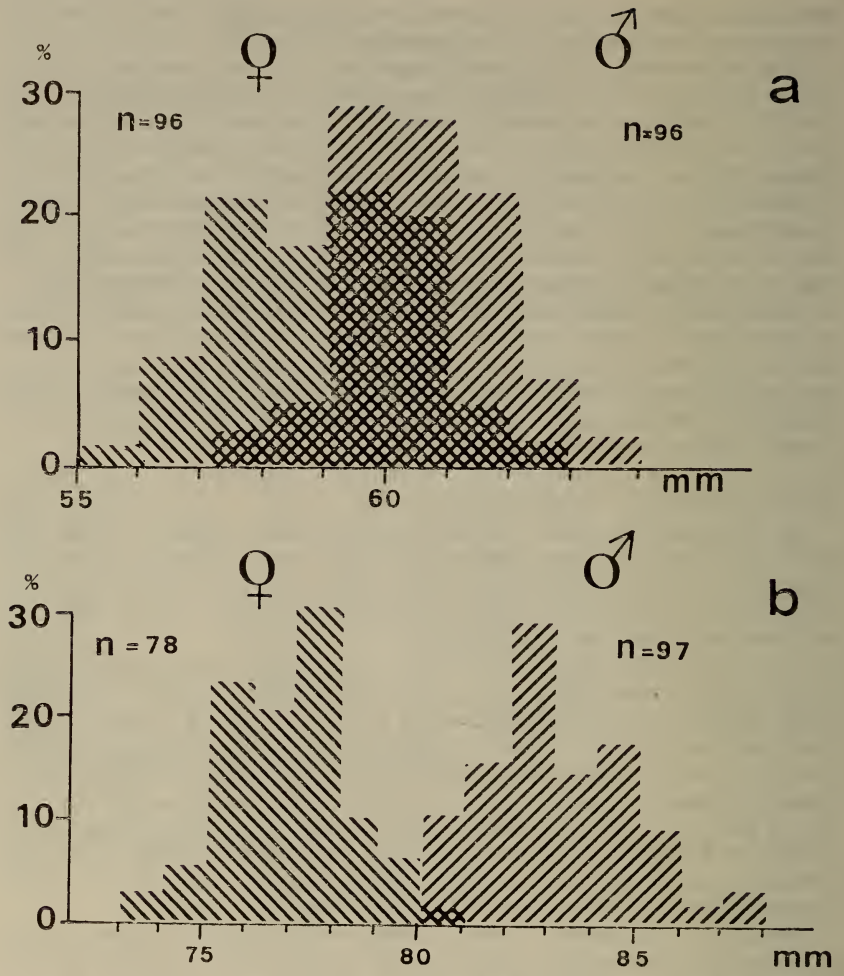
Sexual dimorphism in wing-length

In the present analyses, I include only a mean measurement for each individual which has been measured more than once, in order to avoid any bias from the frequent recapture of certain long-lived, highly territorial individuals. However, in determining overall ranges, I have taken all recorded measurements into account.

For only 4 of the 17 species in Table 1 does there seem to be a complete dimorphism in size between the sexes. The samples for both Fülleborn's Black Boubou *Laniarius fuelleborni* and the Green-headed Sunbird are too small for this to be confirmed. Although there is no overlap in measurements of known male and female Olive-breasted Mountain Bulbuls *Andropadus tephrolaemus*, a large number of unsexed birds have wing-lengths of 95–97 mm, and so there probably is an overlap in fact. The sexual dimorphism in wing-length in the Yellow-streaked Bulbul *Phyllastrephus flavostriatus* is paralleled by differences in weights reported from several populations—a feature of most species in this genus (Britton 1972).

In those 13 species with some overlap in the ranges of wing-lengths for the sexes, the amount of overlap varies considerably. Two extremes are illustrated in Fig. 1: in the Yellow White-eye *Zosterops senegalensis* there is a very broad overlap, and some 92% of all birds measured had wing-lengths of 57.5–62 mm inclusive. On the other hand, only 4% of all Starred Robins had wings of 80–80.5 mm. Proportions overlapping in other species ranged from 6% to 96% (Table 1). It is of interest that 2 of the species that are strongly dimorphic in plumage (Cape Batis and Red-faced Crimson-wing) have an overlap in wing-length of 90% or more.

No other measurement seems to be as suitable as wing-length for distinguishing the sexes. Although tail-lengths of Starred Robin adults are also significantly longer in males, there is a greater degree of overlap between the sexes. This is also true of wing- and tail-lengths combined, which I have analysed, following the suggestion by Oatley (1982) that there was no overlap between the sexes in this measurement in Natal. Dealing only with individual Starred Robins sexed by cloaca, tails overlapped between 61 and



Histograms showing sexual dimorphism in wing-lengths of 2 montane forest passerines on the Nyika Plateau: (a) Yellow White-eye *Zosterops senegalensis*; (b) Starred Robin *Pogonocichla stellata*. The % is shown of each sample falling within each 1 mm of wing-length.

63.5 mm (comprising 16% of the population), and wings+tails between 141 and 144.5 mm (9%).

Sexual dimorphism in weights

The significant differences in wing-length between the sexes in several species are doubtless a reflection of differences in body size. However, it is difficult to establish a direct relationship between an individual bird's wing-length and weight. In part this is because weight varies seasonally much more than does wing-length, but even when comparable data are available, there may still be no apparent relationship (Clark 1979, Snow & Snow 1963).

A sample of 78 adult male Starred Robins measured in October and

November (lacking any apparent furcular fat deposit), when tested statistically gave a low value for the correlation of wing-length with weight (r=0.28). Similarly, there was no significant correlation between these parameters in 39 fat-free adult male Eastern Double-collared Sunbirds, measured when not moulting or breeding (r=0.38). Analyses could not be undertaken for other species of which large samples were measured because of the seasonal presence of visible fat deposits (Dowsett & Dowsett-Lemaire in prep.).

TABLE 3

Sexual differences in weight (g) in some Malawi forest passerines

	Adult male			Adult female		
	n	Range	Mean	n	Range	Mean
Alcippe abyssinica	4	18.3–21.3	20.0	4	18.5–21.0	19.4
Andropadus tephrolaemus	40	32.2–42.0	38.4	90	30.0–41.0	36.8
Phyllastrephus flavostriatus	11	28.1–35.8	31.8	14	22.0–32.4	25.2
Alethe fuelleborni	17	41.6–56.5	49.0	10	44.0–58.0	49.7
Cossypha anomala	28	22.6–27.4	25.0	39	20.6–27.4	24.1
C. caffra	35	26.2–34.0	28.9	23	25.4–32.0	28.0
Pogonocichla stellata	114	16.1–21.5	18.5	93	15.5–26.3	18.7
Turdus olivaceus	11	66.0–77.0	70.8	13	64.5–78.0	70.6
Chloropeta similis	8	10.9–12.7	11.8	5	11.1–14.0	12.6
Apalis thoracica	20	10.9–13.3	12.1	54	10.2–16.0	12.1
Batis capensis	36	11.4–13.6	12.6	34	11.3–15.6	13.1
Elminia albonotata	23	8.4–10.9	9.5	21	7.9–11.6	8.9
Laniarius fuelleborni	6	46.0–53.0	48.9	4	43.0–47.0	45.2
Nectarinia verticalis	5	12.9–15.5	14.2	4	11.8–14.8	13.5
N. mediocris	48	7.2–10.7	8.8	44	6.3– 9.9	7.8
Zosterops senegalensis	96	9.3–12.3	10.7	97	8.9–14.1	11.2
Cryptospiza reichenovii	23	11.5–14.8	13.0	22	11.9–15.6	13.4

Not surprisingly, overall weights (Table 3) of the 17 species in Table 1 show very much more variation and much more overlap between the sexes than do wing-lengths. Even in species showing no overlap in wing-length, such as the Yellow-streaked Bulbul, there may be a large overlap in weights, the heaviest individuals usually being females containing eggs. Although such individuals can be recognised in the hand with experience, those with ovaries at an earlier stage of development usually cannot. Consequently, any analysis of geographical or sexual variation in weights would be biased if samples cannot be strictly comparable, e.g. sexed accurately, not breeding, fat-free and not moulting.

Individual weights of adult forest birds on the Nyika are generally lowest when young are still dependent and also during the cold months (at least in insectivores), and highest just before breeding and afterwards, even during moult (Dowsett & Dowsett-Lemaire in prep.). Seasonal variation may be considerable: for example, female Starred Robins increase weight before saying to some 144% of their minimum weights, and even in males the maxima may often exceed 120% of minimum weights. Diurnal variation in this and species of similar size on the Nyika is in the region of 6.5% of body weight (Dowsett in press).

Discussion

The significant differences in wing-length between the sexes of many of the montane forest birds studied on the Nyika suggest there may be significant differences in body size, despite the difficulty of demonstrating differences in body mass. There may consequently be differences in the size of food eaten, but it is difficult to take this any further. Differences in wing-length may be paralleled by differences in bill-length: for example, bill-lengths of adult male Starred Robins are significantly greater than those of adult females (Student's t-test, $P<0.001$, samples $n=31$ and 16 respectively). However, the differences are rather small, amounting to no more than 1 mm (8%) on average (16.7 *vs* 15.7 mm), and whether they have any practical importance is not known.

In the Nyika forests there are important inter-specific differences in body mass between a few species that might be expected to compete ecologically; but most species are segregated ecologically, and there is little evidence of inter-specific competition (Dowsett-Lemaire in press).

Whether the extent of sexual dimorphism shown here differs significantly from that in similar or related species at lower altitudes (for example, in the larger avifaunas of lowland forests) is not known in the absence of comparable studies elsewhere.

Acknowledgements. This research was undertaken while I was in receipt of grants from the South African Nature Foundation and the Frank M. Chapman Memorial Fund, for which I am most grateful. Some of the data presented are from a thesis which fulfilled part of the requirements of an M.Sc. degree at the University of Natal, and I thank Prof. G. L. Maclean for his supervision. Dr. F. Dowsett-Lemaire has kindly commented on a draft of this paper.

References:

Benson, C. W., Brooke, R. K., Dowsett, R. J. & Irwin, M. P. S. 1971. *The Birds of Zambia.* London: Collins.
Britton, P. L. 1972. Weights of African bulbuls (Pycnonotidae). *Ostrich* 43: 23–42.
Clarke, G. A. 1979. Body weights of birds: a review. *Condor* 81: 193–202.
Dowsett, R. J. In press. Diurnal weight variation in some montane birds in south-central Africa. *Ostrich.*
Dowsett, R. J. & Dowsett-Lemaire, F. 1980. The systematic status of some Zambian birds. *Gerfaut* 70: 151–199.
Dowsett-Lemaire, F. In press. Ecological and territorial requirements of montane forest birds on the Nyika Plateau, south-central Africa. *Gerfaut*
Dowsett-Lemaire, F. & Collette, P. 1980. Weight variations of adult Marsh Warblers (*Acrocephalus palustris*) during the breeding cycle. *Vogelwarte* 30: 209–214.
Flegg, J. J. M. & Cox, C. J. 1977. Morphometric studies of a population of Blue and Great Tits. *Ringing & Migration* 1: 135–140.
Moreau, R. E. 1966. *The Bird Faunas of Africa and its Islands.* London: Academic Press.
Oatley, T. B. 1982. The Starred Robin in Natal Pt.. 1: Behaviour, territory and habitat. *Ostrich* 53: 135—146.
Snow, D. W. & Snow, B. K. 1963. Weights and wing-lengths of some Trinidad birds. *Zoologica* 48: 1–12.
Stewart, I. F. 1963. Variation of wing-length with age. *Bird Study* 10: 1–9.
Svensson, L. 1975. *Identification Guide to European Passerines.* Stockholm: Naturhistoriske Riksmuseet.
Thorne, C. J. R. 1975. Wing length of Reed Warblers. *Wicken Fen Group Rep.* 7: 10–13.

Address. R. J. Dowsett, Rue de Bois-de-Breux 194, B-4500 Jupille, Liège, Belgium.